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Sensitivity Profiles of *Mycosphaerella graminicola* and *Phytophthora infestans* Populations to Different Classes of Fungicides*

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Abstract: Prior to the use of fungicides, the baseline sensitivity of individuals in a pathogen population may already differ by a factor of 10 to 100 between the least and the most sensitive isolates. In *Mycosphaerella graminicola* populations, this factor, measured *in vitro*, was 5 to 20 for both the strobilurin analogue azoxystrobin (baseline) and the triazole cyproconazole which has been in use for several years. In *Phytophthora infestans* populations, this factor, measured in a leaf disc assay, was about 100 for azoxystrobin (baseline), up to 1000 for the cyanoacetamide cymoxanil and >10 000 for the phenylamide oxadixyl; both of the latter have been used for many years. In *M. graminicola*, cross-sensitivity was present between all azole fungicides for the majority of the isolates, whereas no correlation was found between triazoles and azoxystrobin. Despite the existence of cross-sensitivity between azoles, 'box-and-whiskers' plots revealed large variations in the sensitivity profiles of some triazoles; isolates resistant to triazoles have not been detected in *M. graminicola* populations. In *P. infestans* populations, the proportion of the phenylamide-resistant sub-population increased during the season more rapidly in treated than in untreated fields, but it was low at the beginning of the next season in all fields. During disease epidemics, the fitness of phenylamide-resistant *P. infestans* isolates, as characterised by lesion size, was higher than that of the sensitive isolates, but after the overwintering period, the recovery of resistant isolates was apparently lower. The presence of both A1 and A2 mating types of *P. infestans* in European populations, although at different frequencies, allows sexual recombination and increased genetic diversity, affecting sensitivity and fitness. Such mixed populations can still be adequately controlled by using sound anti-resistance strategies.

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1 INTRODUCTION

The application of fungicides to control fungal disease eliminates, in most cases, the majority of the pathogen population present in the crop. Nevertheless, a small part of the population will survive because of inadequate fungicide coverage of some plant parts, and because some individuals of the pathogen population may be less sensitive to the fungicide prior to the application. Also, new inoculum appears in the crop by migration from neighbouring fields which have not been treated at all, or not at the same time. The pathogen population will start to grow again mainly because the original amount of fungicide decreases through degradation and, consequently, repeated applications may be necessary, especially for fast-growing populations. The most sensitive sub-populations are well controlled, but less sensitive and resistant sub-populations are less affected or not controlled at all; they may increase in frequency, especially when the selection pressure is strong and persistent.

Prior to the use of fungicides, the baseline sensitivity of individuals in a pathogen population may already vary by a factor of 10 to 100 between the most and the least sensitive isolate.[1] The first step in the selection process is caused by the fungicide and may result in the survival and increase of less sensitive isolates. These may become dominant as long as the selection pressure persists, but decrease in frequency once fungicide applications are terminated. In such situations the less sensitive individuals are (by definition) less fit than the wild-type population. The second step in the selection process is not related to sensitivity of isolates but favours individuals with higher fitness attributes, e.g. with shorter incubation period and sporulation time, or with a larger lesion size and sporulation capacity. In order to understand the dynamics of fungicide-treated populations, it is of equal importance to monitor the sensitivity of treated and untreated populations as well as to follow epidemiological parameters like fitness, virulence, mating type behaviour and frequency of sexual recombination. Investigations on the genetic background of the mode of resistance may contribute to estimates of the risk of product failures due to resistant sub-populations.

In this contribution, the sensitivity profiles of *Mycosphaerella graminicola* (Fuckel) Schroter and *Phytophthora infestans* (Mont.) DeBary populations are described and analysed both for a fungicide not yet used commercially (the strobilurin azoxystrobin), and for fungicides which have been used for many years, such as the cyanoacetamide cymoxanil, the phenylamide oxadixyl and triazole fungicides, e.g. cyproconazole. Cross-sensitivity behaviour between fungicides as well as important epidemiological parameters of treated and untreated populations are presented and discussed.

2 MATERIALS AND METHODS

In all sensitivity assays, fungicides were used as formulated compounds. Examples of four different classes of fungicide were included in the investigations: the cyanoacetamide cymoxanil (500 g kg^{-1} WP), the phenylamide oxadixyl (250 g kg^{-1} WP), the strobilurin azoxystrobin (250 g $litre^{-1}$ SC) and the demethylation inhibitors (DMIs, azole fungicides) cyproconazole (100 g $litre^{-1}$ SL), tebuconazole (250 g $litre^{-1}$ EC), epoxiconazole (125 g $litre^{-1}$ SC), and prochloraz (450 g $litre^{-1}$ EC). A range of four or five fungicide concentrations was prepared with ten-fold dilution steps. The response of the pathogens to the fungicides was rated visually and dose-response curves were constructed with the help of a logit-log computer programme; the EC_{50} (effective fungicide concentration resulting in 50% inhibition of growth or sporulation) was calculated for each isolate. *M. graminicola* (anamorph *Septoria tritici* Rob. ex Desm.) isolates were obtained from pycnidia-bearing lesions of leaves collected from DMI-treated or -untreated fields in several countries over a period of four to eight weeks during several years. The isolation procedure and the in-vitro sensitivity test method on agar plates are described in more detail by Gisi and Hermann.[2] *P. infestans* isolates were obtained from infected leaves (from treated and untreated fields) and placed between two potato tuber halves (for transportation). Sporangia formed after a few days were sufficient in quantity for an immediate sensitivity test without the need for any transfer. The sensitivity test was performed on leaf discs produced from fungicide-treated potato plants as described in the FRAC method-collection by Sozzi *et al.*[3] The fitness evaluation of *P. infestans* isolates was done simultaneously with the sensitivity test on untreated leaf discs of potato, cv. Bintje, inoculated with 25×10^3 sporangia ml^{-1} and incubated at 18°C; the measurements were taken two, three, four and five days after inoculation. For both *P. infestans* and *M. graminicola* the isolates were considered to be bulk samples. For sensitivity and cross-sensitivity tests, as well as fitness analyses, 20 to 260 isolates per country (or test) were used.

3 RESULTS

3.1 *Mycosphaerella graminicola* populations

In wheat, one or two fungicide applications have been made per season for many years to control *M. graminicola*, especially with azole fungicides. Since 1992, isolates of *M. graminicola* populations from different countries have been collected and tested for their sensitivity to cyproconazole. There are no indications of a decreased sensitivity; the width of sensitivity profiles remained unchanged but varied by a factor of 5 to 40

TABLE 1
Sensitivity of *Mycosphaerella graminicola* to Cyproconazole for Isolates from France, Germany England and Switzerland collected between 1992 and 1996

Country	*Year*	*No. of isolates*	EC_{50} (*mg litre*$^{-1}$)			*Width of distribution*
			Mean	*Min.*	*Max*	
France	1994	9	0·11	0·04	0·30	8
	1995	21	0·11	0·02	0·40	20
	1996	76	0·11	0·03	0·32	11
Germany	1994	14	0·11	0·03	0·30	10
	1995	24	0·08	0·03	0·20	7
	1996	22	0·09	0·02	0·14	7
England	1992	259	0·18	0·03	0·90	30
	1993	219	0·15	0·01	0·40	40
	1994	57	0·14	0·05	0·50	10
	1995	87	0·10	0·01	0·40	40
	1996	93	0·10	0·03	0·24	8
Switzerland	1995	9	0·07	0·04	0·20	5
	1996	20	0·07	0·01	0·13	13

(Table 1). The populations have remained unimodal, and no evidence of two classes within the populations has emerged. Isolates outside the unimodal distribution, that may be considered as azole-resistant isolates, have not been detected since 1991 and it is not known whether a shift could have occurred in earlier years. On the other hand, the 'box-and-whiskers' plots revealed rather large variations in the sensitivity profiles for some populations; this variation in both the boxes (50% of population) as well as the whiskers was much more pronounced for tebuconazole than for cyproconazole, although the minimum EC_{50} values were about the same for the two molecules (Fig. 1).

Twenty-four isolates of the 1996 population from France, representing the entire range of sensitivity, were chosen for cross-sensitivity studies. Between all pairs of azole fungicides, cross-sensitivity was present with a correlation coefficient (r) between 0·52 ($P < 0·01$) and

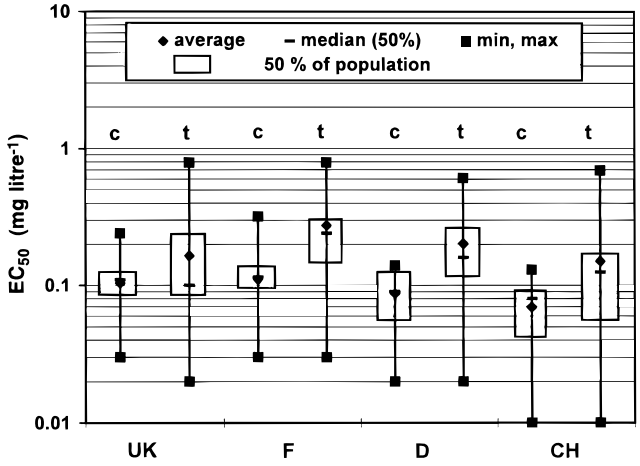

Fig. 1. Sensitivity of *Mycosphaerella graminicola* populations to cyproconazole (c) and tebuconazole (t) in England (UK), France (F), Germany (D) and Switzerland (CH), 1996.

0·86 ($P < 0·001$) (Fig. 2). All regression lines were more-or-less parallel to the transect line of the scatter plots, indicating a similar cross-sensitivity behaviour for all tested isolates, but some azoles displayed a higher intrinsic activity than others (Fig. 2B: epoxiconazole > cyproconazole, 2C: prochloraz > cyproconazole, 2D: epoxiconazole > tebuconazole, 2E: prochloraz > tebuconazole). When entire field populations were tested for cross-sensitivity to the pair tebuconazole/cyproconazole, a correlation between the two fungicides was still present ($r = 0·34$ for France, $r = 0·46$ for England) with high significance levels ($P < 0·01$ and 0·001, respectively), but the cross-sensitivity behaviour was not very pronounced for some isolates, especially for those which were most sensitive to cyproconazole (Fig. 3A).

When isolates from France were analysed for their cross-sensitivity between the triazole cyproconazole and the chemically unrelated strobilurin azoxystrobin, no correlation could be identified ($r = 0·16$, $P > 0·1$) (Fig. 3B). The mean values of the sensitivity distributions as measured by EC_{50} values were 0·04 and 0·11 mg litre^{-1} for azoxystrobin and cyproconazole, respectively, reflecting the different intrinsic activities of the two molecules, whereas the width of the distribution was a factor of 15 and 11, respectively. The *M. graminicola* populations have not previously been exposed to azoxystrobin and therefore, the sensitivity distribution can be considered as a baseline. Although triazoles have been used for many years, the width of the sensitivity distribution to cyproconazole was about the same as that found for azoxystrobin (Fig. 4). There have been no differences in sensitivity distributions of European *M. graminicola* populations to cyproconazole over the last five years (Table 1), not even between treated and untreated fields (results not shown).[2]

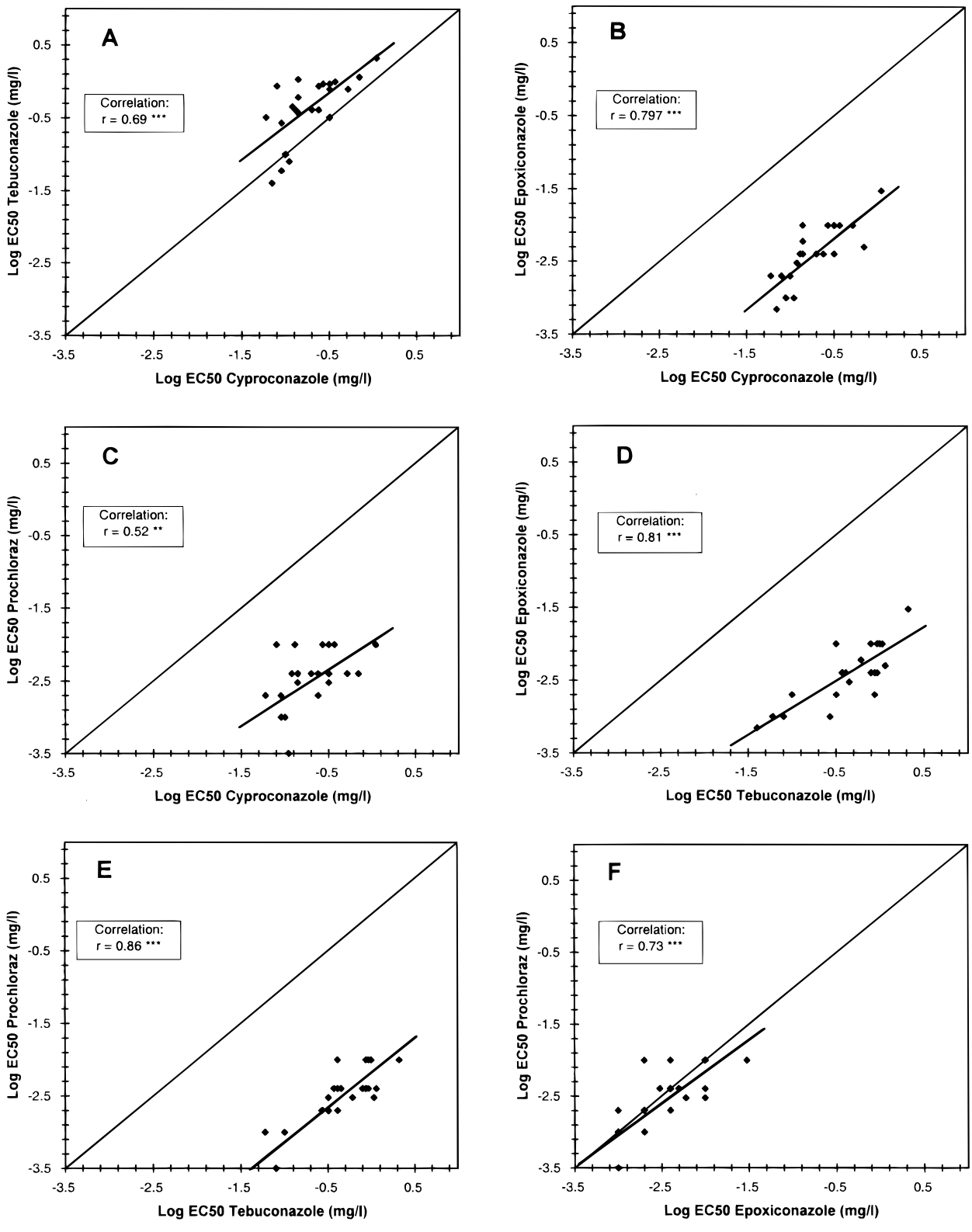

Fig. 2. Cross-sensitivity behaviour in *Mycosphaerella graminicola* to DMI fungicides. A: Cyproconazole versus tebuconazole; B: cyproconazole versus epoxiconazole; C: cyproconazole versus prochloraz; D: tebuconazole versus epoxiconazole; E: tebuconazole versus prochloraz; F: epoxiconazole versus prochloraz. Significance level for correlations: **: $P < 0{\cdot}01$; ***: $P < 0{\cdot}001$ ($n = 24$).

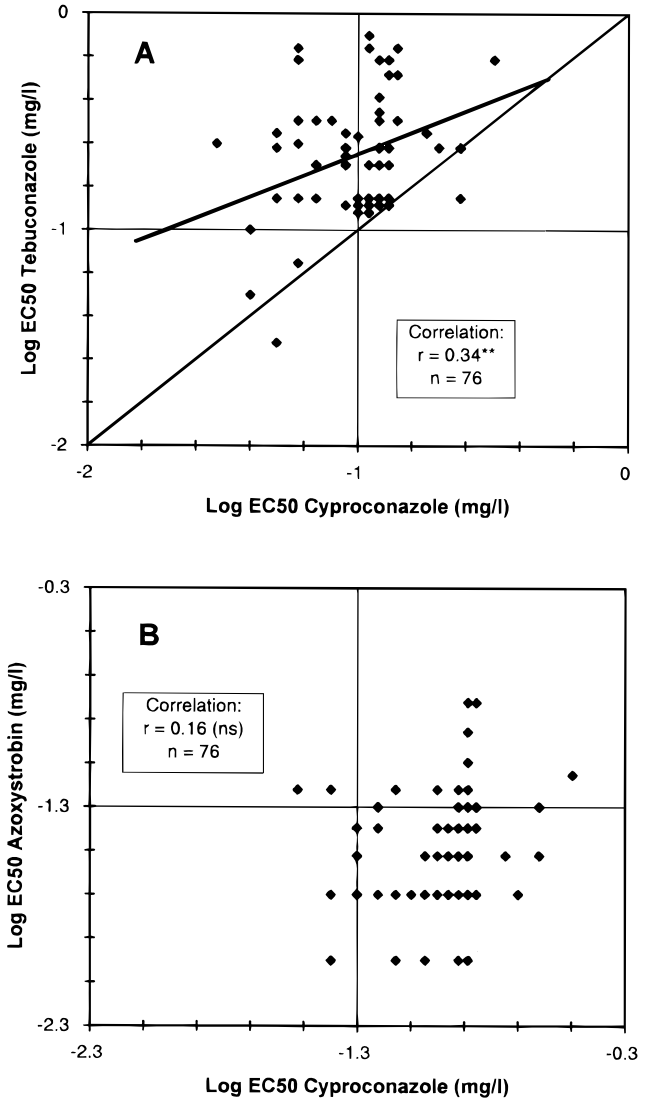

Fig. 3. Cross-sensitivity behaviour in *Mycosphaerella graminicola* isolates from France collected in 1996. A: Cyproconazole versus tebuconazole; B: cyproconazole versus azoxystrobin. Significance level for correlation: **: $P < 0{\cdot}01$; ns: not significant ($P > 0{\cdot}1$).

3.2 *Phytophthora infestans* populations

Several fungicide classes, including products containing phenylamides or cymoxanil, have been used world-wide for many years to control *P. infestans*, the causal agent of late blight in potato and tomato. Both classes are used in combination with contact fungicides (e.g. dithiocarbamates like mancozeb). The strobilurin azoxystrobin is also active against *P. infestans*,[4] but has not been used commercially so far. In a leaf disc assay, the sensitivity of the Swiss *P. infestans* populations of 1996 was determined for the three fungicides, azoxystrobin, cymoxanil and oxadixyl. The baseline sensitivity of isolates to azoxystrobin varied by a factor of up to 100, whereas the sensitivity profiles to cymoxanil and oxadixyl were different by factors of up to 1000 and >10 000, respectively, between the most and the least

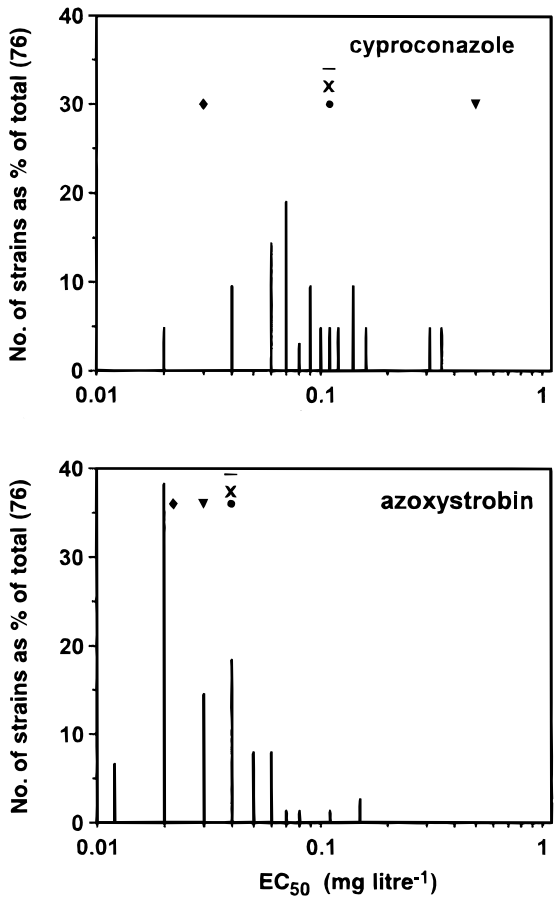

Fig. 4. Sensitivity distribution of *Mycosphaerella graminicola* to cyproconazole and azoxystrobin; isolates from France collected in 1996. (●) mean EC_{50}, (◆) sensitive reference isolate; (▼) reference isolate with decreased sensitivity to triazoles.

sensitive isolate (Fig. 5). For azoxystrobin, no resistant isolates were detected and the population can be described as original log-normal distribution. A large variation for the sensitivity distribution to cymoxanil was observed, but no resistant isolates were found. In mycelial growth tests, this variation can be smaller.[5,6] In contrast, distinct subpopulations with a sensitive, intermediate and resistant response to oxadixyl were present in the Swiss *P. infestans* population (Fig. 5). There is a strong cross-resistance behaviour for *P. infestans* isolates between all phenylamide fungicides (metalaxyl, oxadixyl, benalaxyl, ofurace),[7] but there was no correlation in cross-sensitivity between azoxystrobin and oxadixyl nor between azoxystrobin and cymoxanil for the 105 isolates collected in 1996 in Switzerland (data not shown). Cross-sensitivity analyses between oxadixyl and cymoxanil revealed the presence of isolates with six of the nine possible sensitivity combinations (oxadixyl/cymoxanil: s/s, s/i, i/s, i/i, r/s, r/i), but no isolate contained resistance against cymoxanil (s/r, i/r, r/r) (Table 2). The most dominant subpopulations were those with full sensitivity to both oxadixyl and cymoxanil (s/s = 30%) and those resistant to oxadixyl and intermediate to cymoxanil (r/i = 37%).

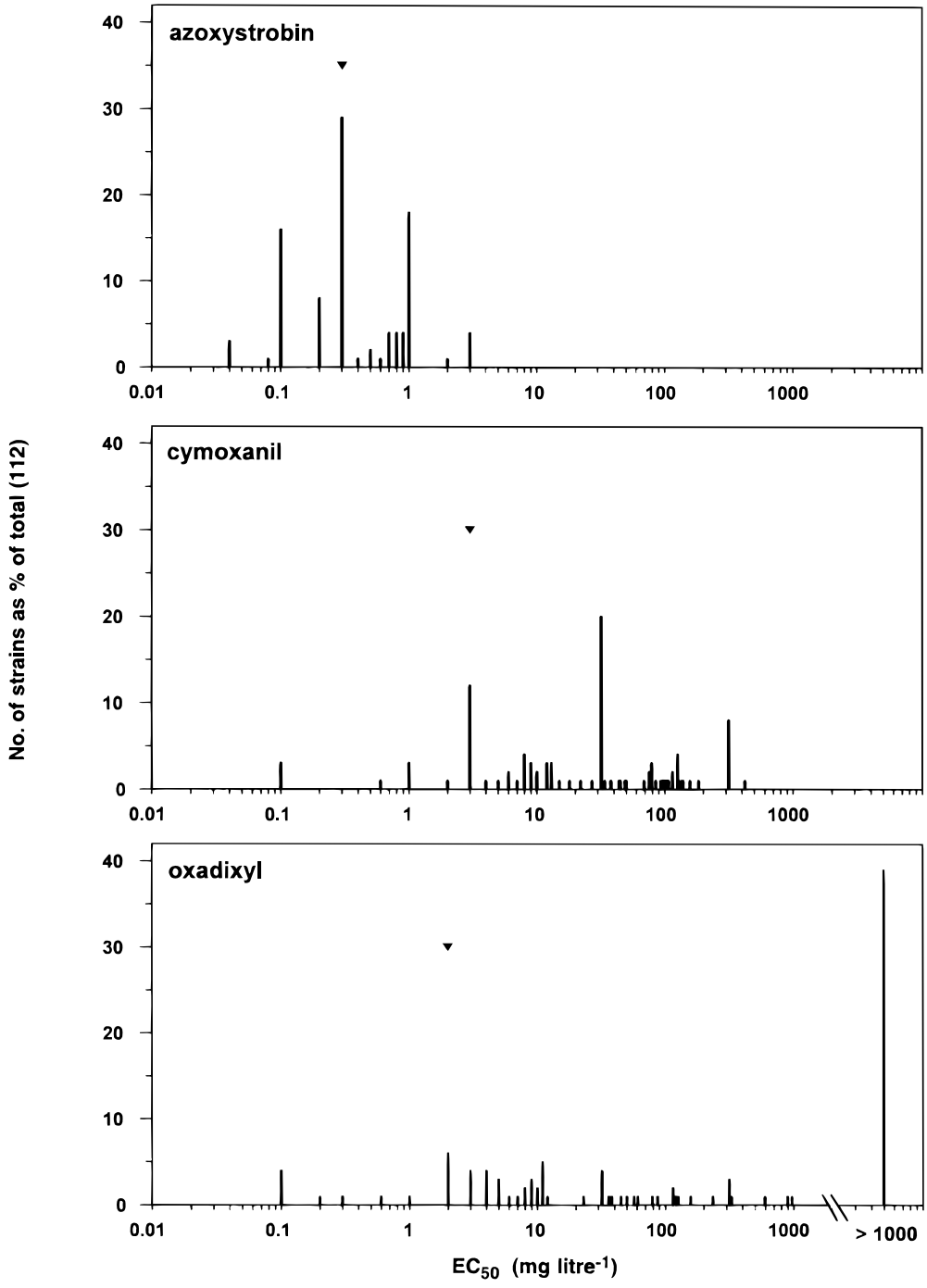

Fig. 5. Sensitivity distribution of *Phytophthora infestans* to azoxystrobin, cymoxanil and oxadixyl; isolates from Switzerland collected in 1996. (▼) mean EC_{50} for sensitive reference isolate.

Over the last ten years, two important epidemiological events occurred in the Swiss (and European) *P. infestans* populations:

(1) At the expense of the resistant sub-population, the proportion of isolates intermediate in sensitivity to oxadixyl (phenylamides) increased from almost nil to about a quarter of the population (Fig. 6). These isolates can be either 'mixed isolates' (s + r, s + i) or genetically stable intermediates (i) to oxadixyl originating from sexual recombination. Since both mating types, A1 and A2, are present in European populations,[8] although in different proportions (e.g. 96% and 4%, respectively, in Switzerland), sexual recombination may occur[9] favouring genetic diversity in populations and thus allow segregation into resistant, intermediate and sensitive sub-populations from populations previously dominated by resistant individuals.[8]

(2) During the epidemic phase of the disease cycle, the proportion of *P. infestans* isolates resistant to phenylamides increases in both treated and

TABLE 2
Sensitivity of *Phytophthora infestans* Field Isolates to Oxadixyl and Cymoxanil in the 1996 population from Switzerland ($n = 112$)[a]

Oxadixyl	*Cymoxanil*	*Proportion* (%)
s	s	30
s	i	8
s	r	0
i	s	7
i	i	16
i	r	0
r	s	2
r	i	37
r	r	0

[a] r, i and s refer to resistant, intermediate and sensitive, with EC_{50} values >1000, >20 but <1000 and <20 mg litre^{-1}, respectively.

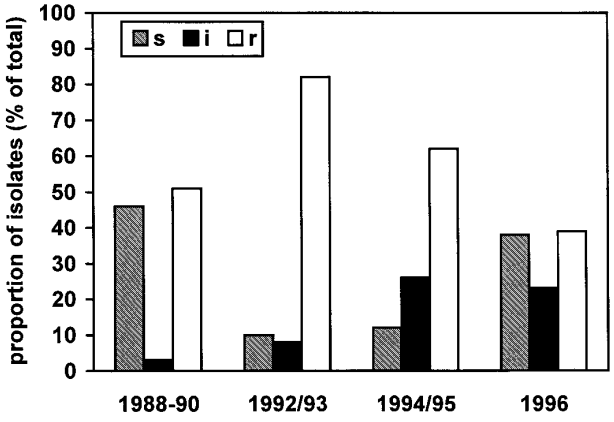

Fig. 6. Proportion of *Phytophthora infestans* isolates (% of total) collected in Swiss potato fields between 1988 and 1996 showing a sensitive (s), intermediate (i) and resistant (r) response to phenylamide fungicides.

untreated populations. Because of fungicide selection pressure, this increase is more rapid in treated compared to untreated potato fields.[8] Nevertheless, at the beginning of the next season, the proportion of the resistant sub-population is again rather low. These observations, made in several countries over many years,[8,10,11] suggest that resistant isolates have a higher fitness during the epidemic phase but are recovered less frequently after the overwintering period of the pathogen.[8] Model trials with mixed populations ($s + r = 9 + 1$) revealed that resistant isolates 'colonise' the potato tissue (leaf during epidemic, tuber during overwintering) much faster than sensitive isolates.[8] In fact, the fitness of *P. infestans* isolates collected in 1996 in Switzerland was higher for the resistant than the sensitive isolates: the incubation period and sporulation time tended to be shorter, whereas lesion size, colonization rate, and thus also the fitness product, were higher for resistant than for sensitive isolates (Table 3).

During the season, the proportion of highly fit isolates slightly increased. The few A2 type isolates tested were somewhat less fit than the A1 isolates (Table 3), which may help to explain the low frequency of A2 isolates in European *P. infestans* populations in potato fields.[8] Preliminary observations revealed a much higher proportion of A2 type isolates in *P. infestans* populations collected from tomato than from potato fields (Knapova and Gisi, unpublished results).

4 DISCUSSION AND CONCLUSIONS

Although azole fungicides have been used for many years for disease control in wheat, no *M. graminicola*

TABLE 3
Fitness Evaluation of *Phytophthora infestans* Field Isolates collected in 1996 in Switzerland

Isolates	*Incubation period* (*day*)	*Lesion size* (mm^2)[a]		*Colonisation rate* ($mm^2\ day^{-1}$)[b]	*Sporulation time* (*day*)	*Fitness product*[c]	*No. of isolates*
		After 3 days	*After 4 days*				
PA-resistant[d]	2·6 (±0·5)	78 (±59)*	299 (±138)**	221 (±108)	3·8 (±0·5)	22·4	43
PA-sensitive	2·7 (±0·5)	58 (±53)*	249 (±143)**	191 (±111)	4·1 (±0·6)	17·2	41
June[e]	2·5 (±0·5)	69 (±59)	256 (±140)	187 (±97)	4·0 (±0·5)	18·7	30
July[e]	2·7 (±0·5)	69 (±57)	279 (±141)	210 (±118)	3·0 (±0·5)	25·9	63
A1	2·6 (±0·5)	69 (±58)	271 (±141)	202 (±112)	3·9 (±0·5)	19·9	103
A2	2·5 (±0·5)	77 (±67)	263 (±195)	186 (±138)	4·0 (±0·6)	18·6	6

[a] */**: significantly different from each other at $P = 0{\cdot}05$ (one-tailed t test).
[b] Difference in lesion size between 3rd and 4th day.
[c] [Colonisation rate]/[incubation period × sporulation time].
[d] PA = phenylamide.
[e] Isolates collected in June or July.

isolates resistant to azoles, i.e. isolates outside the log-normal distribution, have been detected in European populations. Azole fungicides express different intrinsic activities against *M. graminicola*, but there is cross-sensitivity between azoles of the majority of isolates (Fig. 2).[12] Certain azoles may lose some activity against less sensitive isolates earlier than others; therefore, the general cross-sensitivity behaviour may be hidden in some cases. A shift towards a reduction in sensitivity to specific triazoles has been recorded in the UK, but it is unclear whether this shift is seasonal or if it will progressively reduce the overall sensitivity of *M. graminicola* to all triazoles.[13] The width of the sensitivity distribution was about the same for the triazole cyproconazole and the strobilurin azoxystrobin, and both are almost perfect log-normal and unimodal distributions (Fig. 4). Since the distribution profile for azoxystrobin can be considered to be baseline, it is appropriate to claim that, for cyproconazole, no major shifts in sensitivity have occurred so far. As exemplified by cyproconazole, the sensitivity profile of a product with a long spray history may not be more extended than the baseline profile of new chemistry, e.g. the strobilurin azoxystrobin. In contrast, much broader baseline sensitivity profiles have been described for other new fungicides like quinoxyfen in *Erysiphe graminis* DC[14] or the anilinopyrimidine pyrimethanil[1] in *Botrytis cinerea* Pers. ex Fr. It is not known whether different selection processes exist for *M. graminicola* within triazoles as has been claimed to occur in *Rhynchosporium secalis* Davis for triadimenol versus propiconazole.[15]

The sensitivity profile of azoxystrobin was much wider for *P. infestans* (Fig. 5) than for *M. graminicola* populations (Fig. 4), probably because of different testing methods (in-vivo leaf disc versus in-vitro agar plate test). Nevertheless, the *P. infestans* sensitivity profile was much narrower for azoxystrobin (factor of about 100) than for cymoxanil (up to 1000) and for the phenylamide oxadixyl (factor $>10\,000$) (Fig. 5). As discussed by Gisi and Cohen,[8] no genetic link has been found in *P. infestans* between sensitivity to phenylamide fungicides and mating type, nor between sensitivity to phenylamides and fitness. The high proportion of phenylamide-resistant isolates occurred prior to the more frequent appearance of A2 type isolates in Europe.[8] The latter isolates are mostly sensitive, and seem to be less fit than the A1 isolates. Increased fitness of *P. infestans* isolates probably developed soon after phenylamide-resistant isolates were selected from the original population by the use of phenylamide fungicides, otherwise the presence and increase of resistant isolates during the season in fields not treated with phenylamides cannot be explained.[8] Migration of resistant sporangia, or the import in tubers of mycelium resistant to phenylamides, contribute to mixed inocula in untreated fields. In addition, the presence of both A1 and A2 mating type isolates in European *P. infestans* populations allows sexual recombination and this may help establish genetically diverse populations, as well as a mixture of sensitive, intermediate and resistant subpopulations to phenylamides, that may be equally fit. Such mixed populations can be adequately controlled with sound anti-resistance strategies as recommended by the FRAC group.[16]

It is recommended that strong anti-resistance strategies be implemented early in the life cycle of a new class of fungicide. Resistant individuals may exist in original populations prior to the use of fungicides; they are low both in frequency and in fitness at the beginning, but may increase in frequency as a result of the selection process. The first step of this process is imposed by the fungicide but increased fitness may be acquired later through events unrelated to the use of fungicides but through evolutionary processes.

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